Contr. Univ. Mich. Herb. 15:315–324. 1982.

BOTRYCHIUM RUGULOSUM (OPHIOGLOSSACEAE), A NEWLY RECOGNIZED SPECIES OF EVERGREEN GRAPEFERN IN THE GREAT LAKES AREA OF NORTH AMERICA

W. H. Wagner, Jr. and F. S. Wagner
Herbarium and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109

The name *Botrychium ternatum* (Thunb.) Sw. was long applied to the evergreen grapeferns (*Botrychium* subg. *Sceptridium*) of North America. Not until Underwood's pioneering revision of 1898 did there arise any question as to whether true *B. ternatum*, an Asiatic species described originally in 1784 from Nagasaki, Japan, really occurred in North America at all. In his opinion, nothing known to him from the New World could be identified as *B. ternatum*. However, in the late 1950's, Wagner (1959) encountered grapeferns in Michigan that seemed at the time to be the same as, or closely related to, the Japanese species, and its name was once again taken up for certain American collections by various authors. Wherry (1961) referred to the plants in question as the "American ternate grapefern" and described it as "a relative of the Asiatic taxon." Other authors, including ourselves, subsequently simply referred to it as *B. ternatum* without qualification.

In connection with monographic research on *Botrychium* during the past several years, it has become evident that typical *B. ternatum* does not occur in North America, and that the plants that we referred to are distinct from that species in a number of characters. They constitute a new species, closely related to two much more common species that usually occur with it, the endemic American *B. dissectum* Spreng. and the circumboreal *B. multifidum* (Gmel.) Rupr. The purpose of this paper is to describe this new species and to compare it with species of near relationship.

Botrychium rugulosum W. H. Wagner, sp. nov.

Frons deltoidea, 3 (–4)-pinnata, pinnis usque ad apicem divisis, pinnulis ultimis angulatis, oblique rhomboideis, lanceolatis vel oblongis, 0.2–0.5 cm latis, vivis convexis et rugulosis, marginibus grosse dentatis (raro subintegris).

In habit resembling *B. dissectum* and *B. multifidum* with which it usually grows, its fronds emerging from the ground before the former and after the latter. Sterile blades deltoid (Fig. 1, 2) the stalk more or less the same length as the blade (shorter in sun forms, longer in shade forms), the stalk and blade together of mature, fertile plants averaging 8–16 cm (3 cm in sun to 30 in shade), the blade itself averaging 4–8 (2–16) cm long. Sterile blade 3–(2–4)-pinnate, divided to the pinna tips with regular reduction in symmetry. Lateral and basal pinnae ovate-deltoid, the pinnules rhomboidal, ovate, or oblong, usually strongly angled, 0.2–0.5 cm wide, the laminar surface in the living state convex above and more or less coarsely rugulose (Fig. 1, Wagner 1962, Pl. 1). Pinnule margins with nearly regular, somewhat rounded, wide teeth (except in rare

FIG. 1. Frond of *Botrychium rugulosum* (Michigan: Gratiot Co., w. of Meridian Rd., Fall, 1981). Note rugulose and convex segments, indicated by arrow.

subentire forms) (Fig. 2). Lateral veins mainly somewhat spreading rather than nearly parallel (Fig. 3). Chromosomes $n = 45$.

TYPE: U.S.A., MICHIGAN, Midland Co., Mills Twp., south side of Baker Road, sect. 29, R. 2E, T. 16N. Common in more or less open, dry, sandy field with scattered trees and shrubs, east of oil well. 9 September 1959. *W. H. Wagner 9099, M. Sargent, and R. L. McAdams.* (MICH).

Botrychium multifidum (Gmel.) Rupr. f. *dentatum* R. Tryon (1939) is a synonym, based upon compact forms of *B. rugulosum* from northern Wisconsin.

COLLECTIONS EXAMINED

CANADA: ONTARIO: CARLETON CO.: Merivale, *Minshall s.n.*, no date (DAO). MIDDLESEX CO.: Near London, *Balkwill, J.A. s.n.*, 10 Oct 1893 (MICH.) MUSKOKA CO.: Georgian Bay I, Beausoleil I, *Stirrett 1212*, no date (DAO). NORTHUMBERLAND CO.: Castleton, *Macoun, J. s.n.*, Aug 1860 (NY). COUNTY UNKNOWN: Lake region and Ontario, *Macoun, J. s.n.*, 15 Aug 1874 (MTMG).

QUEBEC: CHAMBLY CO.: Chambly, *no collector*, 25 Sep 1927 (MTMG). GATINEAU CO.: Ironside, Hull, *Rolland-Germain 97*, no date (MTMG). RICHELIEU CO.: St-Joseph-de-Sorel, *Marie-Victorin, F 28082*, 23 Sep 1928 (GH). STANSTEAD CO.: Hatley, *Mousley, H. s.n.*, 1919 (US). TERREBONNE CO.: Terrebonne, *Terrill s.n.*, 23 Oct 1927 (MTMG). VAUDREIL CO.: Rigaud, *Robert, C.S.U. s.n.*, no date (DAO).

UNITED STATES: CONNECTICUT: WINDHAM CO.: Brooklyn, *Merritt, A.O. s.n.*, Oct 1903 (MICH).

MICHIGAN: BENZIE CO.: Sect 1, NW Shorter Lake, *Hagenah, D.J. 6585*, 12 May 1967 (BLH). CHIPPEWA CO.: Sugar I, Sect 33, *Hiltunen, J.K. 2695*, 4 Sep 1960 (MICH.) CLARE CO.: Sect 16, 17, S side Rte 115, *Wagner, W.H. et al. 63193*, 14 Nov 1963 (MICH). GRAND TRAVERSE CO.: Sand Lake, *Wagner, W.H. et al. 9389*, 22 May 1961 (US). SE Traverse City, Sect 28, *Wagner, W.H. & F.S. 9451*, 5 Jul 1961 (MICH). SE Traverse City, unnamed lake, *Wagner, W.H. et al. 9316, 9319, 9322*, 1 Oct 1960 (all MICH). Sect 29, T 27 N, R 9 W, *Hagenah, D.J. 4516*, 1 Oct 1960, *4614*, 3 Jun 1961 (both BLH). 11 mi ESE Traverse City, beach small lake, *Dieterle, J.V. 1981*, 4 Sep 1960 (MICH). GRATIOT CO.: Sect 25, ½ mi S M-46, W of Meridian Rd, *Wagner, W.H. & F.S. 9442*, 2 Jul 1961, *Wagner, W.H. et al. 8679* 12 Apr 1959, *9108*, 20 Sep 1959 (all MICH). IOSCO CO.: Sect 5, T 23

FIG. 2. Sterile frond silhouettes of eastern North American *Botrychium* subg. *Sceptridium* (all MICH). R = *B. rugulosum* (Michigan): (1) Monroe Co., *8670*, (2) St. Clair Co., *Hagenah H-S-T*, (3) Monroe Co., *8594*, (4) Monroe Co., *8598*, (5) Coarse form, Monroe Co., *8594*, (6) Saginaw Co., *70503*; (7) Juvenile form, Monroe Co., *8598*, (8) finely cut form, Muskegon Co., *Voss 9180*. M = *B. multifidum* (Michigan): (1) Keweenaw Co., *McVaugh 11146*, (2) Wexford Co., *9314*. D = *B. dissectum* (Indiana): (1) Jefferson Co., *D. M. Smith SDM-5-1*, (2) the same, *SDM-2C-1*, (3) Dissected extreme, the same, *SDM-3A-B*. (All field nos. without collector designated are W. Wagner).

N, R 5 E, *Wagner, WH. et al. 9329*, 2 Oct 1960 (MICH). JACKSON CO.: ½ mi ENE Trist & Seymour Rds, *Wagner, W.H. 73460*, 13 Oct 1973 (MICH). KALKASKA CO.: Sect 14, 4 mi W Kalkaska, *Hagenah, D.J. 4606*, 3 Jun 1961 (BLH). KENT CO.: Lake Shore Dr 1 mi S Kent City, *Wagner, W.H. et al. 9205a*, 23 Apr 1960 (BLH, MICH). LEELANAU CO.: NW Cook Lake, Sect 35, *Hagenah, D.J. 6582*, 12 May 1967 (BLH). LIVINGSTON CO.: Near Lime Lake, *Wagner, W.H. et al. 62358*, 26 Oct 1962 (MICH). S side Sayle's Lake, *Wagner, W.H. 8417*, 27 Jun 1957 (MICH). MIDLAND CO.: E side Jefferson Rd near Shearer, *Wagner, W.H. & Blasdell, R.F. 8999*, 3 Jun 1959 (MICH). Sect 29, NW ¼, E of oil well, *Wagner, W.H. et al. 9029*, 11 Jun 1959, *9099*, 9 Sep 1959,*9258*, 14 Jul 1960 (all MICH).

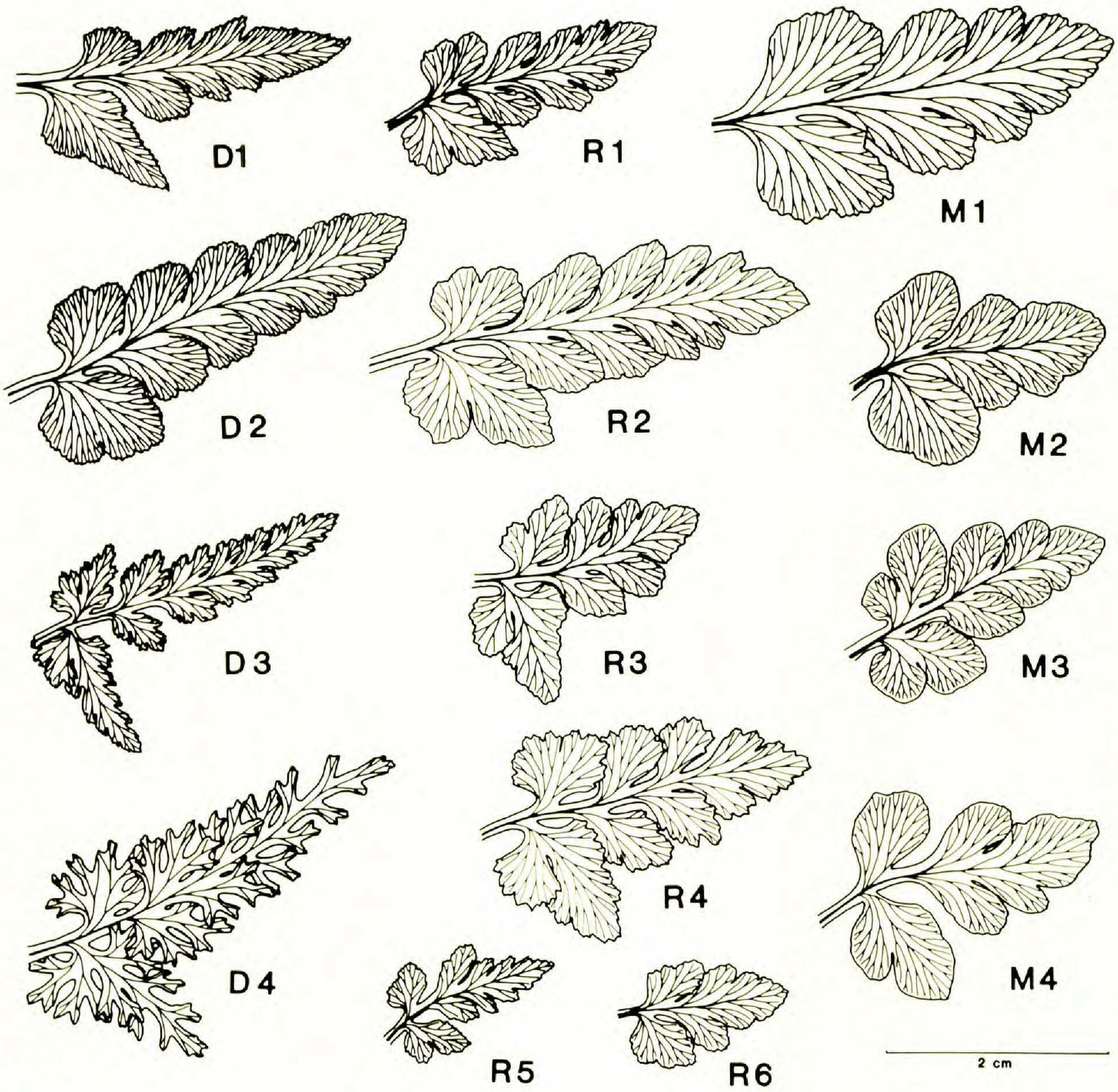

FIG. 3. Segment shapes and venation patterns of eastern North American *Botrychium* subg. *Sceptridium* (all MICH). R = *B. rugulosum* (Michigan): (1) Monroe Co., *8603*, (2) Monroe Co., *9123*, (3) Gratiot Co., *9108*, (4) Midland Co., *9099*, (5) same as (1), (6) same as (4). M = *B. multifidum* (Michigan): (1) Midland Co., *9097*, (2) same as (1), (3) Mecosta Co., *9116*, (4) St. Clair Co., *9053*. D = *B. dissectum*: (Michigan): (1) Monroe Co., *8596a*, (2) Cheboygan Co., *8063a*, (3) Midland Co., *9096*, (4) (Canada, Ontario): Kent Co., *9158*. (All field nos. are W. Wagner.)

W side Sect 15, Kawkawlin R, *Hagenah, D.J. 4623*, 10 Jun 1961 (BLH). MISSAUKEE CO.: Sect 22, T 23 N, R 7 W, *Hagenah, D.J. 5027*, 11 Aug 1962 (BLH). MONROE CO.: Dixon Rd, 2 mi NE Petersburg, *Wagner, W.H. 8396b*, 11 Jun 1957, *9067*, 12 Jul 1959, Wagner, W.H. & BLASDELL, R. F. *8594*, 16 Sep 1958 (all MICH). Grames Rd near Tuttle Hill Rd, *Wagner, W.H. 8598*, 16 Sep 1958, *Wagner, W.H. & McAdams 9126*, 9 Oct 1959 (both MICH). Ida Twp, *Wagner, W.H. & Hauke, R. & K. 8632*, 2 Oct 1958, *Wagner, W.H. & McAdams 9123*, 9 Oct 1959 (both MICH). Ida Twp, E of US-23 near irrigation ditch, *Wagner, W.H. 8670*, 14 Nov 1958, *Wagner, W.H. & Blasdell, R.F. 8649*, 18 Oct 1958, *Wagner, W.H. & Hagenah, D.J. 8635*, 4 Oct 1958, *Wagner, W.H. & McAdams 9123*, 9 Oct 1959, *Wagner, W.H. et al. 8670*, 14 Nov 1958, *9261*, 4 Aug 1960, *s.n.*, 2 Nov 1961 (all MICH). Plank Rd near Ostrander Rd, *Wagner, W.H. & White, R.A. 9100–3*, 16 Sep 1959 (MICH). Rutherford's, Dixon Rd, *Wagner, W.H. & Blasdell, R.F. 8594*, 16 Sep 1958, *Wagner, W.H. & Sargent, M 9066*, 5 Jul 1959 (both MICH). Sect 5, Hitchingham Rd, *Blasdell, R.F. 300*, 12 Oct 1958 (MICH). W of Plank Rd, N of Ostrander Rd, *Wagner, W.H. & Shetler, S. 8603*, 19 Sep 1958 (MICH). MONTCALM CO.: E of 131, S of Mecosta Co, *Wagner, W.H. et al. 9114*, 26 Sep 1959 (MICH). MUSKEGON CO.: Gerber Scout Reservation, *Wagner, W.H. 9249*, 5 Jul 1960 (MICH). NW of Holton, *Voss, E.G. 9180*, 13 Sep 1959 (MICH). OGEMAW CO.: Sect 29, T 23 N, R 3 E, *Wagner, W.H. et al. 9326*, 2 Oct 1960 (MICH). OSCODA CO.: Wagner Lake, *Wagner, W.H. 70163*, 30 Apr 1970 (MICH). Wagner Lake, Sect 13, *Hagenah, D.J. 6039*, 21 Apr 1963 (BLH). SAGINAW CO.: Fordney Rd, *Wagner, W.H. et al. 9048*, 21 Jun 1959 (MICH). Fordney Rd, N of Brady Rd, *Wagner, W.H. et al. 8589*, 15 Sep 1958, *9045–5*, 21 Jun 1959 (both MICH). SAGINAW CO.: M-46, S of Hess Rd, *Wagner, W.H. 70503*, 4 Nov 1970 (MICH). Nehmer's Woods, W of Saginaw, *Case, F. s.n.*, 25 Sep 1958 (MICH). Rte 85, 5 mi S

Frankenmuth, *Churchill, J.A. s.n.*, 20 Aug 1956 (MSC). 1⅓ mi E Burt, *Wagner, W.H. et al. 8586*, 15 Sep 1958 (MICH). 1/5 mi S Gratiot Co line, *Wagner, W.H. et al. 8683*, 12 Apr 1959 (MICH). 2¾ mi N Chapin, *Wagner, W.H. et al. 9104*, 20 Sep 1959 (MICH). 6/10 mi N Birch Run Rd, *Wagner, W.H. 8520*, 22 Mar 1958 (MICH). ST CLAIR CO.: Algonac, *Farwell, O.A. 3552–5*, 12 Oct 1913, *7260*, 15 Oct 1924 (both BLH). E side Wales Rd, *Wagner, W.H. et al. 9305*, 23 Aug 1960 (MICH). N side Nolan Rd, *Wagner, W.H. et al. 62010*, 31 Mar 1962 (MICH). N side Rte 21, *Wagner, W.H. 9055*, 26 Jun 1959, *9311*, 23 Aug 1960 (MICH). NE edge Algonac, *Wagner, W.H. et al. 9163*, 20 Dec 1959 (MICH). Nolan Rd, Hagenah, D.J. H-S-T, 11 Nov 1961 (MICH). TUSCOLA CO.: Swaffer & Bray Rds, *Wagner, W.H. & Barnes 8616*, 23 Sep 1958 (MICH). WASHTENAW CO.: Waterloo Rec Area, N of Cedar Lake, *Wagner, F.S. 81026*, 12 May 1981 (MICH). 1 mi NE Willis McKean Rd, *Grether, D.F. s.n.*, 6 May 1956 (MICH). WAYNE CO.: Center Sect 30, Sumpter Twp, *Wagner, W.H. & Blasdell, R.F. 8614*, 22 Sep 1958, *Wagner, W.H. et al. 9194a, 9194b*, 30 Mar 1960 (all MICH). Huron R Dr, junct Flat Rock, I-94, *Wagner, W.H. & Morzenti 9220*, 20 May 1960, *Wagner, W.H. et al. 8640–5*, 11 Oct 1958 (both MICH). Merriman Rd, near Pennsylvania Rd, *Wagner, W.H. 9347*, 12 Mar 1961 (MICH). N side Oakville-Wally Rd, *Wagner, W.H. 62095*, Jun 1962 (MICH). Sect 11, off Willis Rd, *Blasdell, R.F. 299*, 3 Oct 1958 (MICH).

MINNESOTA: AITKIN CO.: N side Rte 200, 5 mi E Cass Co, *Wagner, W.H. & F.S. 79316–1*, 28 Jul 1978 (MICH).

NEW YORK: HERKIMER CO.: Dutch Hill, 6 mi E Utica, *Haberer, J.V. 1901*, Nov 1905 (US). MADISON CO.: Lenox, Oneida Lake, *Haberer, J.V. s.n.*, Oct 1906 (US). ST LAWRENCE CO.: Parishville, *St John, E.P. s.n.*, 11,21 Sep 1942 (US). 3 mi SW Parishville, *St John, E.P. s.n.*, 28 Jul 1943 (US). 3 mi W Parishville, *St John, E.P. s.n.*, 2 Aug 1943 (MICH).

VERMONT: ADDISON CO.: Base Green Mt, Middlebury, *Brainerd, E s.n.*, 8 Sep 1899 (NY). Bristol, *Hosford, F.H. s.n.*, 26 Sep 1878, *Pringle, C.G. s.n.*, 26 Sep 1878 (both NY). Bristol, Cobble Hill, *Brainerd, E s.n.*, 12 Sep 1900 (MO). Mt Philo, *Wagner, W.H. & Lellinger, D.B. 9084*, 19 Aug 1959 (MICH). CALEDONIA CO.: St Johnsbury, Harris Hill, *Rooney, B.M. s.n.*, 22 Oct 1903 (US). St Johnsbury, Padduck Village Cemetery, *Rooney, B.M. s.n.*, 9 Oct 1902 (US). CHITTENDEN CO.: Hinesburgh, *Hosford, F.H. s.n.*, 22 Sep 1880 (NY,US). FRANKLIN CO.: Fletcher, *Tryon, R.M. 4642*, 14 Oct 1939 (MO). 1+ mi W Fletcher intersect, *Wagner,W.H. & Lellinger, D.B. 9087*, 19 Aug 1959 (MICH). ORANGE CO.: Randolph Center, *Denslow, H.M. s.n.*, 9 Sep 1910 (NY). ORLEANS CO.: 1½ mi S Morgan, Seymour Lake, *Harper, J.S. s.n.*, 31 Aug 1932 (NY). RUTLAND CO.: Rutland, *Eccleston, W.W. s.n.*, 27 Sep 1893 (NY). WINDSOR CO.: Woodstock, Billings Hill, *Kittredge, E.M. s.n.*, 14–23 Sep 1930 (MICH).

WISCONSIN: BAYFIELD CO.: Barnes Twp, Sandbar Lake, *Peck, J.H. s.n.*, 21 Sep 1979 (UWL). Sand lake near Barnes, *Tryon, R.M. 4100*, 14 Jul 1938 (WIS). Sect 31, NW ¼, T 45 N, R 8 W, *Moran, R.C. 125752*, 3 Sep 1980 (MIL). DOUGLAS CO.: Black Fox Lake, *Somerville, M.F. 71*, 20 Sep 1930 (WIS). Cheney Lake, *Somerville, M.F. 47*, 10 Sep 1931 (WIS). Deer Print Lake, *Somerville, M.F. 44*, 20 Sep 1930 (WIS). Gordon, *Somerville, M.F. s.n.*, 1 Sep 1929 (MO). Gordon, 2nd beach sand lake, *Somerville, M.F. s.n.*, 1 Sep 1929 (MICH). Lower Eau Claire Lakes, *Somerville, M.F. 55*, 5 Sep 1932 (WIS). N of sand lake, *Peck, J.H. s.n.*, 17 Jul 1979 (UWL). Sand lake, *Conklin & Somerville 1180–83*, 6 Sep 1938 (WIS), *Fisher, M 79–81*, 17 Jul 1979 (Pigeon Lake Field Station), *Fuller, A.M. 3926*, 6 Aug 1930 (MIL), *Somerville, M.F. s.n.*, 25 Jul 1931 (WIS). Sand lake near Barnes, *Tryon, R.M. 4100*, 14 Jul 1938 (WIS). Sand lake on 2nd beach, *Somerville, M.F. s.n.*, Sep 1938 (MIN). Sand lake, 1st & 2nd beaches, *Conklin & Somerville 109595a*, 6 Sep 1938 (MIL), *1182* (WIS), *1187* (US). Smith Lake, *Somerville, M.F. 49*, 21 Aug 1931 (WIS). 12 mi E Solon Springs, sand lake on county H, *Tryon, R.M. & P.F. 4336*, 4 Jul 1940 (MO). MARINETTE CO.: Near Peshtigo, *Grassl, C.O. 7393*, 2 Sep 1936 (MICH). PORTAGE CO.: N of Almond, *Thomson, J.W. s.n.*, 24 Aug 1938 (WIS). WAUSHARA CO.: Sand lake, *Sorenson 2660*, 17 Jul 1962 (WIS).

Various aspects of the systematic biology of *B. rugulosum* (identified as *B. ternatum*) are dealt with by Wagner (1959, 1960a,b, 1961, 1962a). This is a very rare fern, in spite of the many localities recorded in the range map, Fig. 4. It seems to be most numerous in Vermont and Michigan, but this may be due in part to the intensive collecting in these two states. At the majority of places there are only one or a few individuals, occurring with related species which are much more common. It grows associated with other members of subgenus *Sceptridium*: in its northern occurrences mainly with *B. multifidum* and in its southern occurrences with *B. dissectum*. In Michigan we deliberately set out to discover sites, and invariably we found either *B. multifidum* or *B. dissectum* first and then searched for *B. rugulosum*. We suspect that there are many localities yet to be discovered, especially in southern Ontario, the Upper Peninsula of Michigan, and northern Wisconsin.

Figure 5 presents the results of thorough collecting in 24 places in south-

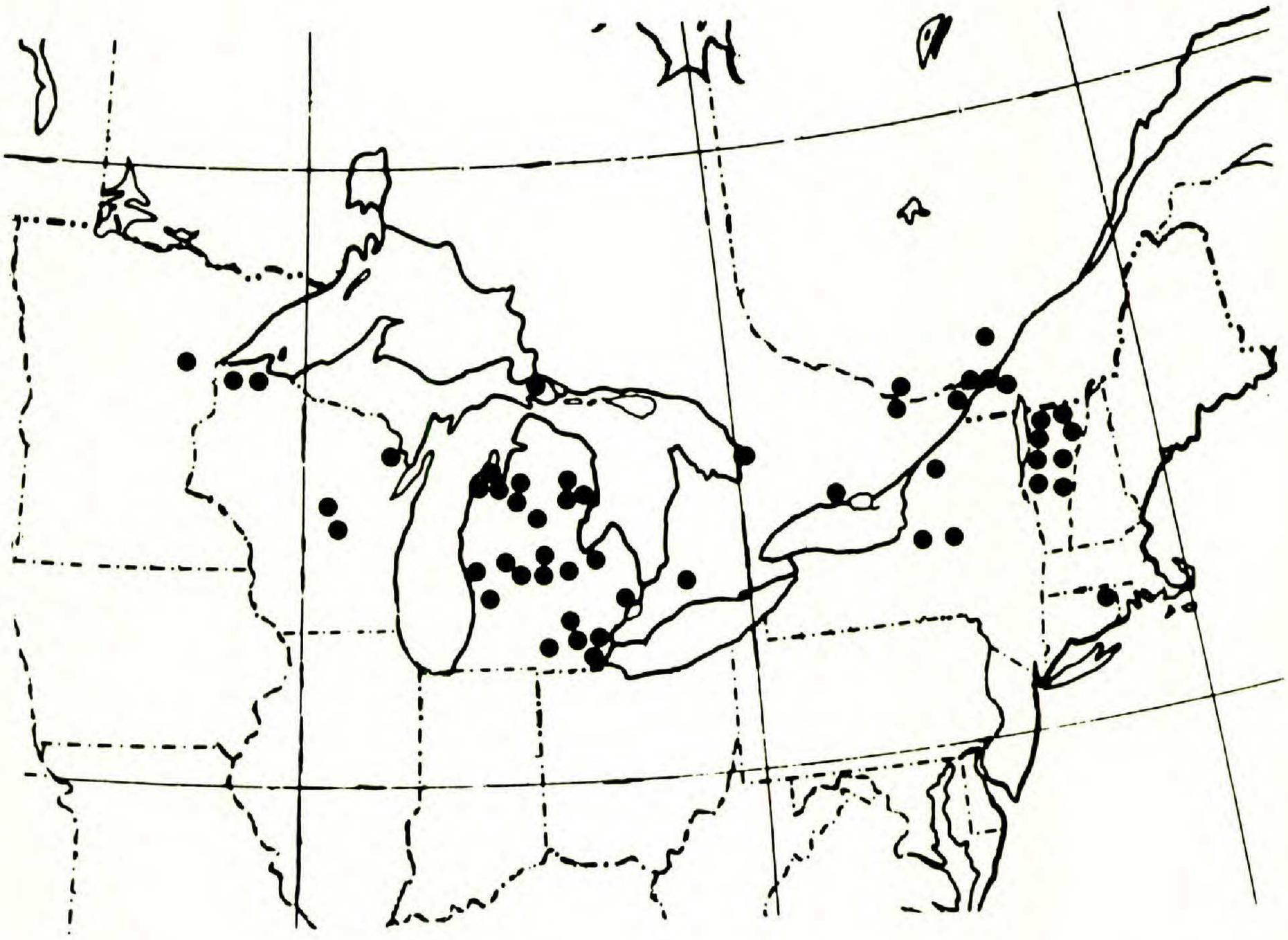

FIG. 4. County distribution map of *Botrychium rugulosum* based on herbarium collections.

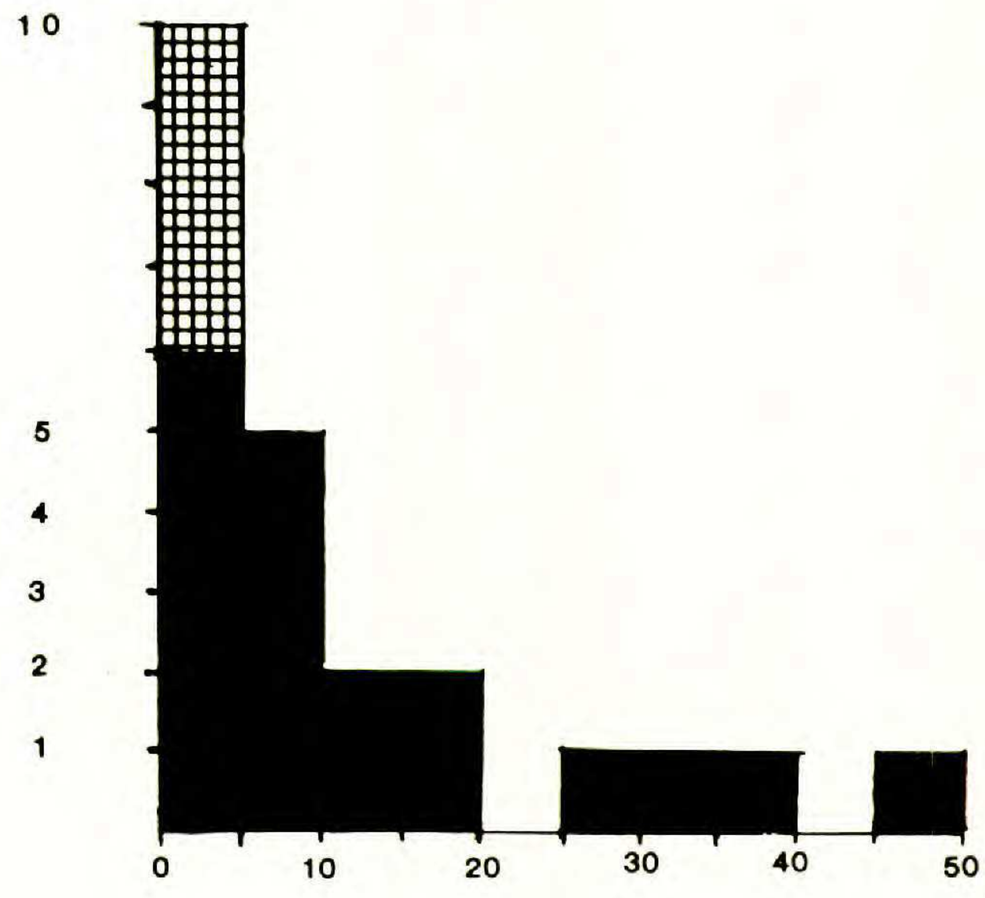

FIG. 5. Bar graph of incidence of plants of *B. rugulosum* in 24 localties in southeastern Michigan. Y axis = number of localities; X axis = no. of plants. (Single locality with 130 plants not shown).

eastern Michigan from Midland County south to Monroe County, and including eight counties altogether. The bar graph gives the number of localities that produced progressively 1–5, 6–10, and so on, plants. The best spot (Monroe Co., 2 mi. n. e. of Petersburg, *W. Wagner 8594*, (MICH)) yielded 130 specimens; it is not shown on the graph. As will be seen, however, most of the habitats gave far less. Indeed, 15 of them had ten or less individuals, 62.5 percent of the total, and 6 (25 percent) (shown in black in first bar) had only one! The survey, which was made over a three-year period (1957–1959), gave results which have since been repeatedly confirmed. This means that if a large stand of evergreen grapeferns of more common species is discovered, it should be carefully examined, for there

may be one or a few *B. rugulosum* mixed in. The median number per locality in our survey was seven, and the mean 17. *Botrychium dissectum* was found in all 24 localities, *B. oneidense* (Gilb.) House in 12, and *B. multifidum* in 11. If our survey had been made in northern Michigan or Wisconsin, *B. dissectum* and *B. oneidense* would probably have been uncommon or absent, and *B. multifidum* would be invariably present.

The substratum in all localities is sandy or silty with more or less included black organic matter. The soil evidently ranges from circumneutral to acidic, more commonly the latter. In the southern portion of the range, *B. rugulosum* is found mostly in low swampy areas, especially in old second-growth grassy places and along paths. Past grazing evidently stimulates the formation of populations. Old apple orchards abandoned for twenty or more years provide productive sites, as do brushy old fields and second-growth upland woods. In Vermont and New York actively pastured open fields and meadows have proved to be ideal and in these places we have frequently been interrupted in our studies by the visits of curious cows. The grazing does not seem to have any serious effects on the plants, although some of them appear trampled and many are dwarfed. The most dwarfed and compact sun forms of *B. rugulosum* and other sceptridiums occur in open, exposed grassy areas around and near borders of sandy lakes as in northern Michigan (especially Grand Traverse Co.) and northern Wisconsin (Douglas Co.), where its most common associate is *B. multifidum*.

In the more northern localities for *B. rugulosum* the haircap moss, *Polytrichum*, is usually abundant, associated with low shrubs such as *Gaultheria procumbens* and *Rubus hispidus*. Other woody plants found with it are generally scattered or clumped, and include *Acer rubrum, Betula papyrifera, Hamamelis virginiana, Populus tremuloides, Prunus serotina, Salix* spp., *Spiraea alba,* and *Vaccinium angustifolium*. Also found are such herbaceous genera as *Antennaria, Fragaria, Hieracium, Lycopodium, Osmunda, Pteridium,* and *Solidago*.

In southern localities (as illustrated in Michigan in the region from Saginaw and St. Clair counties to Monroe Co.), grapeferns grow in richer sites as a rule, and the plants of *B. rugulosum* reach the largest size known, some of the sterile fronds attaining 25 or more cm in length (Wagner, 1959, pl. 9). Associated with the fern in these richer sites are such woody taxa as *Acer rubrum, Cornus drummondii, C. racemosa, C. stolonifera, Corylus americana, Populus tremuloides, Sassafras albidum, Ulmus americana,* and *Vitis riparia*. Among the herbs are species of *Anemone, Aster, Desmodium, Equisetum, Fragaria, Solidago,* and *Viola*. The spleenwort fern, *Asplenium platyneuron,* has in recent years become one of its most frequent associates.

The actively grazed pastures that we studied in Franklin Co., Vermont, and in St. Lawrence Co., New York, contain much more freshly disturbed conditions than the foregoing. The botrychiums tend to be most common in the most open areas, where the cattle trample some and perhaps nibble some. Trees occur mainly at the edges in the less disturbed parts of the pastures. Where grazing is most intense, the plants of *B. rugulosum* may occur in almost lawn-like habitats. Clumped vegetation is produced by *Dennstaedtia punctilobula, Pteridium aquilinum, Rubus idaeus, Comptonia peregrina, Spiraea alba, S. tomentosa,* and *Juniperus virginiana*. Colonies of these species overtop the other vegetation which is made up of such genera as *Achillea, Antennaria, Danthonia, Fragaria, Gnaphalium, Hieracium, Lycopodium, Panicum, Plantago, Poa, Polygonum, Polytrichum, Prunella, Rumex,* and *Viola*.

In localities for *B. rugulosum* we often encounter not only one to three other species of evergreen grapeferns, but the moonworts, *B. matricariifolium* and *B. simplex*, the rattlesnake grapefern, *B. virginianum*, and the northern adder's-tongue, *Ophioglossum vulgatum* var. *pseudopodum*. At the type locality for *B. rugulosum* there were seven species of *Botrychium* plus the *Ophioglossum*. The

seasonal sequence of leaf development in the four species of Great Lakes evergreen grapeferns is in the order (1) *B. multifidum*, (2) *B. oneidense*, (3) *B. rugulosum*, and (4) *B. dissectum* (Wagner 1960, 1961). Leaf development in all of these ferns is exceptionally slow, taking 3–4 months from the time of appearance of the young frond above ground in May or June and the maturation of the leaf and sporangia in September and October. The contrasts are striking in mixed populations in late June and July when the species differ widely in the extent of leaf development. *Botrychium rugulosum* new leaves average 1.3–1.8 times as developed as those of *B. dissectum* during June and July. During the same period the young leaves of *B. multifidum* are approximately 2–4 times further developed than those of *B. rugulosum*. The same phenological differences exist in respect to sporangial maturation in the fall, as measured by the changes in sporangial color from green to yellow to brown, although these changes are more variable than the early vernation changes.

Once a field botanist becomes familiar with the characters of *B. rugulosum* it is unlikely that he will confuse it with any of the three other members of subg. *Sceptridium* that occur in the Great Lakes area. A key to these is given below. Of all the species, *B. rugulosum* has the most slender appearance and a somewhat thinner texture. Although over-all frond size is extremely variable both within and between populations, *B. rugulosum* can be told immediately from *B. dissectum* because it lacks the long undivided terminal segment of the pinna tips (Figs. 2, 3). All of the pinnules of *B. rugulosum* tend to be smaller than those of *B. dissectum* and are usually only one- to two-thirds as large. In the wild the distinctive rugulose and convex pinnule surfaces of *B. rugulosum* are especially valuable in distinguishing it from *B. dissectum*. The bizarre dissected form of *B. dissectum* is connected by intermediates to the "normal" form, f. *obliquum*. Some of the intermediates can occasionally be confused with *B. rugulosum*, unless the pinnule shapes are carefully examined. Even though they may be rather finely cut, the forms of *B. dissectum* always show the outline of the long terminal segments. Those of *B. rugulosum* are not only evenly divided to the tip, but the tips tend to be blunter. *Botrychium rugulosum* is readily separated from *B. multifidum* by its smaller segments; their strongly angular, rather than rounded, outlines (Fig. 3); their rugulose, rather than smooth, surfaces (Fig. 1); and the marked differences in timing of vernation (Wagner, 1960a). Unfortunately the spores of all of these grapeferns are variable, and we have not yet been able to find differences dependable enough to use in routine identification.

The true *B. ternatum* of Japan is a plant of wooded hillsides, pathways, and grassy terraces. It is more finely divided than *B. rugulosum*, and the ultimate divisions tend to be linear, linear-lanceolate, or lanceolate-ovate, with their sides more parallel. The segments are not only narrower, but their margins are beset with delicate, very narrow, pointed teeth, these of very different shape, as a rule, from those of *B. rugulosum*. The texture of *B. ternatum* is generally thinner and more herbaceous than that of *B. rugulosum*. Smith (1967) found in an analysis of their phenolic compounds that *B. ternatum* is more similar to *B. japonicum* (Prantl) Underw., and that *B. rugulosum* is more similar to *B. dissectum*. *B. ternatum* differs from *B. rugulosum*, according to Smith, in presence or absence of six phenolic compounds.

Of other New World sceptridiums that might be confused with *B. rugulosum* only *B. schaffneri* Underw. of Mexico southward is likely to cause any problems. It is a plant of pine woods and pastures at high altitudes with pinna outlines more narrow and more sharply deltoid than in *B. rugulosum*. The primary pinnules are more contracted basally, and the median and submedian pinna bases are more inequilateral, the basiscopic first pinnule becoming nearly sessile on the rachis, the acroscopic first pinnule remote from the rachis. The sterile segments of *B. schaffneri* are slightly more divided, the ultimate pinnules more distant, smaller, and commonly unequally bifid with the acroscopic lobe larger.

Chemical evidence found by Smith (1967) indicates closer relationship of *B. schaffneri* to other southern and tropical American taxa (*B. lunarioides* (Michx.) Sw. and *B. jenmanii* Underw.) than to any other botrychiums.

DISCUSSION

Botrychium rugulosum is unquestionably a distinct species, and the combination of its geographical range, periodicity, blade cutting, segment shapes, laminar contours and marginal teeth set it apart from all other species of subg. *Sceptridium*. The populations of *B. rugulosum* are consistent in repeating the specific characters uniformly in over 70 localities in an area of the Great Lakes region that extends approximately 1000 miles (1600 km) from Minnesota in the west to Connecticut in the east. Most importantly, *B. rugulosum* grows intermixed with other sceptridiums in the same habitats. It exists side-by-side with *B. dissectum* and *B. multifidum* and sometimes *B. oneidense* as well. The distinctive characters of *B. rugulosum* are therefore not merely environmental modifications.

It is intriguing to speculate on the origin of this species. How is it possible for a species to be limited to an area that 15,000 years ago was completely covered by Wisconsin glaciation? We might also ask the same question about the rare and local little goblin fern, *B. mormo* W. Wagner, of northern Michigan, Wisconsin, and Minnesota (Wagner & Wagner, 1980). There are a number of possible hypotheses to explain these ranges. Among them we can propose explanations invoking (1) long-distance dispersal, (2) allopatric speciation, (3) relicts, and (4) migration.

As to long-distance dispersal by spores, our original idea that *B. rugulosum* was actually the same as the Asiatic *B. ternatum* is now abandoned and an assumption that we had received this species in the New World from spores carried by prevailing winds from the west is now without support. We know of no place in the world today, other than the Great Lakes region, where there are plants that conform to *B. rugulosum*. The second hypothesis involving *de novo* evolution of a new species following glaciation also seems questionable. It is difficult for us to imagine a new species of *Botrychium* based on a number of characters (Wagner 1960b) evolving as a result of temporarily localized allopatry independent of its relatives, and then quickly spread over such a wide range.

The hypothesis that *B. rugulosum* may represent a relict that survived in non-glaciated areas does not seem unreasonable, but there is as yet scanty evidence of the role of refugia. The classical idea of nunataks, for example, has usually been contradicted by substantial geological data. On the other hand, *B. rugulosum* may have survived glaciation in, for example, the Driftless Area of Wisconsin, and when the glacier receded and the climate changed, the fern returned eastward and northward to its present range.

To us, the hypothesis of migration southward with the glacial front is at present the most appealing. Recent phytogeographers are inclined to believe that our northern flora was in general shifted southward by glaciation and that, ideed, many if not most species were forced into the middle and southern states. Support for this hypothesis comes largely from pollen core data. If *B. rugulosum* had actually been an ancient northern species that migrated southward at the leading edge of the glacier and then later returned, this picture would not be different from that of numerous well known species, especially of trees.

It is interesting to speculate that *B. rugulosum* may have had something to do with the variation of the enigmatic grapefern, *B. dissectum,* and its origin. The northern *Botrychium rugulosum* might have been forced, during glaciation, into contact with the southern *B. biternatum* that today occurs from the Ohio Valley southward to the Gulf Coast. In some ways *B. dissectum* appears to be intermediate between *B. rugulosum* and *B. biternatum*. Perhaps *B. dissectum* constitutes a

more or less stabilized hybrid swarm at the diploid level. Toward the north it is more similar to *B. rugulosum* and toward the south *B. biternatum*. However, even without f. *dissectum*, *B. dissectum* is considerably more variable than either of them. *B. dissectum* f. *obliquum* would represent the "normal" form of the hybrid and the striking and unique f. *dissectum* with its curiously lacerate pinnules might represent the result of morphogenetic upsets due to genetic conflicts (cf. Wagner, 1962b).

KEY TO GREAT LAKES BOTRYCHIUM SUBG. SCEPTRIDIUM

1. Sterile pinnules deeply and conspicuously lacerate, the ultimate segments linear or narrowly oblong, with mostly 1–2 veinlets. *B. dissectum* f. *dissectum* (intergrades to *B. d.* f. *obliquum*)
1. Sterile pinnules dentate to entire, not lacerate, the ultimate segments wider, mostly ovate, spatulate, or lanceolate, with numerous veinlets.
   2. Terminal pinna divisions more or less undivided, linear lanceolate to ovate; plants becoming more frequent south of 43° N.
      3. Plants of various habitats; terminal pinna blades elongate, linear-lanceolate to lanceolate, acute; lamina exposed in winter tending to become bronzy; roots dominantly dark and corky, av. 2.5 mm thick (dried) 1 cm from stem; new leaves appearing in early June. *B. dissectum* f. *obliquum*
      3. Plants of low, shaded forests and swamps; terminal pinna blades ovate-lanceolate to ovate, rounded; lamina exposed in winter remaining dull green; roots dominantly ivory- to tan-colored, smooth, av. 2.0 mm thick (dried) 1 cm from stem; new leaves appearing in middle May. *B. oneidense*
   2. Terminal pinna divisions regularly divided to the tips, plants becoming more frequent north of 43° N.
      4. Pinnules rounded, larger, mostly 4–8 mm wide; the living lamina flat; pinnule margins mostly finely crenate to entire; new leaves appearing in early May. *B. multifidum*
      4. Pinnules angular, smaller, mostly 2–5 mm wide; the living lamina convex and rugulose; pinnule margins mostly coarsely dentate; new leaves appearing in late May. *B. rugulosum*

ACKNOWLEDGMENTS

We are grateful to the many individuals who helped us in the field, the herbarium curators who lent us specimens, and those persons who provided us relevant information about where these plants might occur. We thank David J. Bay and Joseph M. Beitel for their help with the illustrations, and we give special thanks to Kerry S. Walter for his aid in providing computer programs for collection data. W. R. Anderson translated the diagnosis into Latin. This research was carried out in large part under NSF Grant DEB 8005536 for Evolution and Systematics of *Botrychium*.

LITERATURE CITED

Smith, D. C. 1967. Chemical characters as a guide to the taxonomy of Botrychium. Doctoral thesis, University of Michigan, Ann Arbor.

Tryon, R. M., Jr. 1939. Notes on the ferns of Wisconsin. Amer. Fern Jour. 29: 1–9.

Underwood, L. C. 1898. American ferns—1; the ternate species of Botrychium. Bull. Torrey Bot. Club 25: 521–541.

Wagner, W. H., Jr. 1959. American grapeferns resembling Botrychium ternatum: a preliminary report. Amer. Fern Jour. 49: 97–103.

———. 1960a. Periodicity and pigmentation in Botrychium subg. Sceptridium in the northeastern United States. Bull. Torrey Bot. Club. 87: 303–325.

———. 1960b. Evergreen grapeferns and the meanings of infraspecific categories as used in North American pteridophytes. Amer. Fern Jour. 50: 32–45.

———. 1961. Some new data on the vernation differences of *Botrychium dissectum* and *B. ternatum*. Amer. Fern Jour. 51: 31–33.

———. 1962a. Plant compactness and leaf production in Botrychium multifidum "ssp. typicum" and "forma dentatum." Amer. Fern Jour. 52: 1–18.

———. 1962b. Irregular morphological development in hybrid ferns. Phytomorphology 12: 87–100.

——— and F. S. Wagner. 1981. New species of moonworts, Botrychium subg. Botrychium (Ophioglossaceae) from North America. Amer. Fern Jour. 71: 20–30.

Wherry, E. T. 1961. The Fern Guide. Doubleday and Co., New York.